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Distribution of demersal fish assemblages along the west coast of St Lucia: Implications for planning no-take marine reserves

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Abstract

1. Evidence-based decisions relating to effective marine protected areas as a means of conserving biodiversity require a detailed understanding of the species present. The Caribbean island nation of St Lucia is expanding its current marine protected area network by designating additional no-take marine reserves on the west coast. However, information on the distribution of fish species is currently limited.
2. This study used baited remote underwater stereo-video to address this shortcoming by investigating the effects of depth and seabed habitat structure on demersal fish assemblages and comparing these assemblages between regions currently afforded different protection measures.
3. From the 87 stations visited a total of 5,921 fish were observed comprising 120 fish taxa across 22 families. Species richness and total abundance were higher within the highly managed region, which included no-take reserves. Redundancy analysis explained 17% of the total variance in fish distribution, driven predominantly by the seabed habitats. The redundancy analysis identified four main groups of demersal fishes each associated with specific seabed habitats.
4. The current no-take marine reserves protected two of these groups (i.e. fishes associated with the 'soft corals, hard corals or gorgonians' and 'seagrass' groups). Importantly, habitats dominated by sponges, bacterial mats, algal turfs or macroalgae, which also supported unique fish assemblages, are not currently afforded protection via the marine reserve network (based on the five reserves studied). These results imply that incorporation of the full breadth of benthic habitat types present would improve the efficacy of the marine reserve network by ensuring all fish assemblages are protected.

KEYWORDS

biodiversity, Caribbean, coral, fish, marine protected area (MPA), RDA, seagrass, stereo-BRUV, subtidal

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1 | INTRODUCTION

Anthropogenic stressors are increasingly degrading many marine ecosystems around the world (Halpern et al., 2015), with concomitant ecological alterations such as habitat restructuring or loss (Stuart-Smith et al., 2018), depletion of fish stocks (Myers & Worm, 2003; Edgar, Ward & Stuart-Smith, 2018) and reduction of biodiversity (Worm et al., 2006; Elahi et al., 2015). At a societal level, these changes negatively impact the essential goods and services (e.g. provision of food, protection of livelihoods and maintenance of environmental resilience) that marine ecosystems provide (Halpern et al., 2015; McCauley et al., 2015).

Similar to terrestrial environments, the implementation of protected areas in marine ecosystems is one approach aimed at stemming further degradation (Kelleher & Kenchington, 1991; Edgar et al., 2014; Pereira et al., 2017). Marine protected areas (MPAs) vary widely in the types of protection measures and restrictions that can occur within their boundaries. For example, no-take marine reserves are MPAs wherein fishing activity is totally prohibited as a tool to protect fish biodiversity. The ecological benefits of no-take marine reserves such as increases in the size, diversity, density and biomass of fished organisms are well documented (Garcia-Charton et al., 2008; Lester et al., 2009). In recent years, MPAs have been widely implemented to support biodiversity conservation and as a potential fisheries management tool (Botsford, Micheli & Hastings, 2003; Russ et al., 2004; Chateau & Wantiez, 2009). Fish are the most publicly recognized generators of marine ecosystem services (Holmlund & Hammer, 1999) and marine cultural services, and tourism associated with coral reefs and sandy beaches, for example, has been a primary focus of such management measures (Barbier et al., 2008).

Nevertheless, marine reserves occasionally invoke opposition from local stakeholders as they often have logistical and financial implications (Bavinck & Vivekanandan, 2011; Bennett & Dearden, 2014). Furthermore, through a combination of unclear objectives, poor enforcement and lack of knowledge about changes in species or ecosystem functioning (Boersma & Parrish, 1999; Russ et al., 2004; Eklöf et al., 2009; Edgar et al., 2014; Gill et al., 2017), the effectiveness of marine reserves has been heavily criticized. Consequently, it is becoming increasingly evident that more information is needed, not only to understand the role of marine reserves as a fisheries management and conservation tool, but also to support reserve placement in order to maximize the likelihood of conservation objectives being achieved (Jameson, Tupper & Ridley, 2002; Weeks et al., 2017). Unfortunately, all too often the necessary data may not be available and marine reserve locations are decided, to a large degree, through stakeholder compromise, after considering issues of compliance, governance and 'educated' judgement concerning ecological objectives (Jameson, Tupper & Ridley, 2002; Polunin, 2002).

Tropical shallow water demersal fish assemblages are shaped by complex interactions of biological and physical parameters and are, therefore, generally highly variable at different spatial scales

(Malcolm, Jordan & Smith, 2011). One of the most influential factors in structuring demersal fish assemblages is benthic cover or habitat type (Chabanet et al., 1997; Fitzpatrick et al., 2012; Komyakova, Munday & Jones, 2013), especially where strong differences in habitat structural complexity are observed (García-Charton et al., 2004). Furthermore, a strong correlation between fish assemblages and depth has been observed (Zintzen et al., 2012; Schultz et al., 2014; Andradi-Brown et al., 2016). This inherent relationship between demersal fish assemblages and the environment allows for the adoption of physical and biophysical proxies for variations in fish assemblages which in turn may be used to support the decision-making process for planning of marine reserves. Underlying differences or gradients in such physical proxies are more easily measured, categorized and geo-referenced (Ward et al., 1999; Dalleau et al., 2010) than those of their associated fish assemblages. However, the application of physical surrogates in planning the optimal location and design of marine reserves inherently rests on the assumption that fish distributional patterns consistently correlate with abiotic variables (Schultz et al., 2014).

The Caribbean island of St Lucia is a volcanic isle with a mountainous interior whose population and economic activities are predominantly restricted to its coastal fringe. The marine environment is of fundamental importance to St Lucia's economy and its narrow underwater shelf supports the island's nearshore fisheries resources. The island has a long history of effective marine management (Hawkins et al., 2006) with the valuable but scarce marine resources being recognized as conservation priorities. Following increased concerns in the 1980s and 1990s regarding the detrimental impacts of tourism and fishing around the town of Soufrière and the UNESCO World Heritage designated Pitons Management Area, a local management authority responsible for the adjacent Soufrière Marine Management Area (SMMA) was established. This included the designation of a network of small no-take marine reserves designed to protect reef and mangrove habitats (Evans, Schill & Raber, 2015). The country is currently in the process of developing a marine spatial plan to sustainably maximize Blue Growth while reducing stakeholder conflict, and this is likely to include delineating further no-take reserves.

In this study, we assess the spatial distribution of demersal fish assemblages along the west coast of St Lucia and quantify their relationship with environmental factors (e.g. seabed habitat type, depth). A baited remote underwater stereo-video ('stereo-BRUV' hereafter) approach was used to assess fish distributions. This approach offers a cost-effective, non-destructive technique that avoids the need for divers and reduces inter-observer variability as samples can be reanalysed and validated at a later date (Langlois et al., 2010; Fitzpatrick et al., 2012; Whitmarsh, Fairweather & Huveneers, 2017). Empirical fish distributional data for St Lucia, and how such patterns are governed by environmental drivers such as seabed habitats and depth, were used to not only allow an assessment of the appropriateness of current marine reserves in relation to biodiversity representation, but also to inform management decisions regarding the location

of future reserves. The outcomes of this study will inform conservation planning and management of St Lucia and more broadly about the drivers of biodiversity patterns.

2 | MATERIALS AND METHODS

2.1 | Survey design

The study area, the northern two-thirds of the west coast of St Lucia (Figure 1) were identified through consultation with local stakeholders. This area was classified into three geographical regions (Figure 1). The SMMA in the south was targeted as a currently managed area with greater protection. The coastline between Marigot Bay and the SMMA (Soufrière to Marigot Bay; Figure 1) was identified by the Department of Fisheries as a potential MMA although data to support its management are presently lacking. Finally, the northernmost region ('North of Marigot Bay') is currently unregulated and is included in this study as it provides a suitable area with which to compare the fish populations found in the two managed regions. Furthermore, the data acquired form an important baseline from which subsequent changes can be assessed should protected areas in the

offshore areas (where no reserves are currently located) within North of Marigot Bay be implemented.

While the distribution of seabed habitats was largely unknown at the time of survey, generalized seabed types classified from towed video data were used. Stereo-BRUV stations were positioned to coincide with towed video locations that were based on a grid lattice. A subset of these stations was then targeted across the range of seabed types and depth classes within the three regions. All proposed stations had a maximum depth of ~50 m to ensure sufficient light for identification of fish and spanned across five marine reserves (Figure 1). Other marine reserves in areas shallower than 20 m are present in this region but were unsuitable for BRUV surveying due to high vessel traffic, poor water clarity or hazards on the sea bed.

2.2 | Field methods

The survey was conducted during February 2019 in accordance with the field procedures outlined in Langlois et al. (2020). Sampling used four stereo-BRUVs each consisting of two Sony FDR-X3000 ActionCam cameras mounted within a customized housing supplied

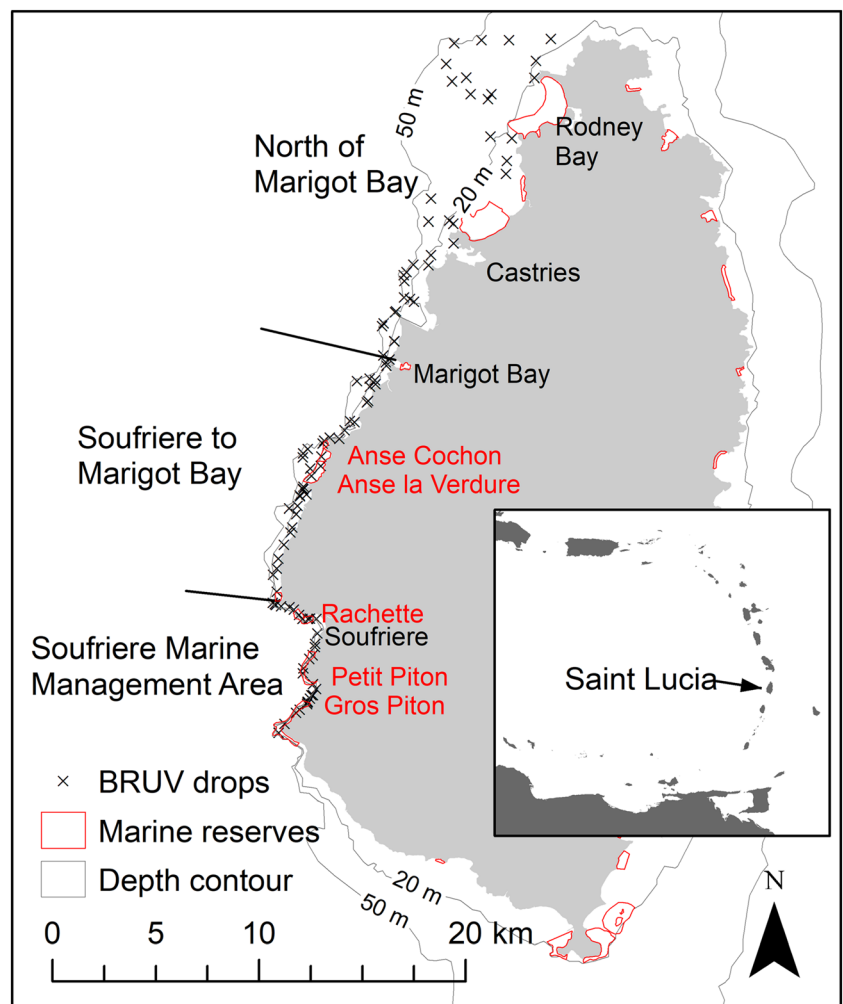


FIGURE 1 Location of baited remote underwater stereo-video (stereo-BRUV) stations across the three regions (solid black lines) along the west coast of St Lucia. Marine reserve boundaries (in red) are approximate based on legislation definitions (Saint Lucia Fisheries Act 2001). The five reserves that were sampled in the present study are named in red text

by SeaGIS. Camera housings were fixed to a steel base bar with a separation of 700 mm and cameras angled inward at 7°. The basebar was built into an aluminium weighted frame and lowered to the seabed with a horizontal field of view of 8 m. A wire mesh bait bag loaded with approximately 1 kg of crushed, locally sourced sardines (replaced between deployments) was fixed to a 1,000 mm bait pole on each frame. The stereo-BRUV systems were calibrated at the start and end of the survey using the calibration cube and CAL software (<https://www.seagis.com.au/bundle.html>).

As each stereo-BRUV approached the seabed the rate of descent was reduced to gently place the frame in the correct orientation without damaging fragile habitat features. A GPS fix was taken the moment the frame touched the seabed and a rope was fixed to a surface buoy to mark its location. Stereo-BRUV systems were deployed for a bottom time of at least 60 min at each station with concurrent deployments being separated by a minimum distance of 500 m. Deployments began at least 1 h after sunrise and the last camera was recovered at least 1 h prior to sunset to avoid crepuscular periods (Langlois et al., 2020). One-hundred and seven stations were sampled, although footage from 20 stations was unusable owing to various factors (e.g. incorrect orientation of BRUV on sea bed, currents too strong; Table 1).

2.3 | Video classification

Video footage was analysed using the software 'EventMeasure' (<https://www.seagis.com.au/event.html>). Footage from the left camera was analysed for the maximum number of individuals for each species in a single frame (MaxN). MaxN is the maximum number of individuals of any one species seen in a single frame and avoids double counting of moving fish (Langlois et al., 2020). Fork length of the individual fish at MaxN was measured in the software packages 'Eventmeasure'; however, the analysis of length data is not presented in this study. Videos were classified by two analysts with 10% of the videos being classified by both analysts to allow comparison and ensure consistency. Based on this quality control procedure, a limited number of inconsistencies in species identification and naming between analysts was identified and these were amended for the entire dataset.

2.4 | Environmental information

Broad substrate classes (e.g. extent of consolidation of substratum), record of the dominant phyla present (e.g. coral, gorgonians, seagrass) (hereafter referred to as 'biogenic habitat') and topographic relief of the habitat were recorded for each station based on the stereo-BRUV field of view. The depth of each station was recorded using the vessel's depth plotter during deployment while the distance from both the shore and from the nearest no-take marine reserve of each station was measured using ArcMap GIS software.

TABLE 1 Summary of environmental characteristics of the 87 baited remote underwater stereo-video (stereo-BRUV) stations

Parameter	Category	Number of stations
Depth	<10 m	21
	10–20 m	23
	20–30 m	19
	30–40 m	18
	40–50 m	6
Substrate type	Continuous consolidated substrate	23
	Patchy consolidated substrate	35
	Seagrass	29
Biogenic habitat	Algal turf	8
	Bacterial mat	4
	Gorgonians	1
	Hard corals	3
	Soft corals	2
	Macroalgae	15
	Seagrass	29
	Sponges	25
Relief	Flat	25
	Low (<1)	40
	Moderate	15
	High (>3)	7
Distance to shore	<100 m	15
	100–200 m	26
	200–500 m	17
	500–1,000 m	13
	1,000–2,000 m	7
	2,000–5,000 m	9
Distance to nearest marine reserve	Inside	14
	<500 m	19
	500–1,000 m	14
	>1,000 m	40
Region	SMMA	20
	Soufrière to Marigot Bay	33
	North of Marigot Bay	34

2.5 | Data treatment and analyses

2.5.1 | Data treatment

The raw data were exported from Eventmeasure as MaxN. Prior to analyses, it was important to truncate the raw data to ensure species counts were not artificially inflated by entries at different taxonomic

resolutions. For example, the single observation of *Canthigaster* sp. across the whole survey was changed to *Canthigaster rostrata* as this species (the only other entry for this genus) was observed 54 times. Meanwhile, where a particular genus entry was commonly observed across the dataset (e.g. *Scomberomorus* sp.), species entries for that genus (e.g. *Scomberomorus regalis*) were truncated to genus level. Finally, taxa which were clearly pelagic (e.g. Carangidae (jacks)) were removed from the dataset.

Except where otherwise specified, all analyses and plots were performed using R software (R Development Team, 2019) (packages 'ade4' (Dray & Dufour, 2007), 'adespatial' (Dray et al., 2020), 'vegan' (Oksanen et al., 2019) and 'tidyverse' (Wickham et al., 2019)) and bespoke functions available in Borcard et al. (2018).

2.5.2 | Univariate metrics and multivariate assemblage structure

The DIVERSE routine in the software PRIMER v7 (Clarke & Gorley, 2015) was used to calculate a suite of univariate metrics (e.g. taxon richness, diversity) of assemblage structure for each station based on MaxN. Following inspection of matrix shade plots, fourth-root-transformation was selected for multivariate analyses to downweight the influence of the small number of numerical dominants in the dataset and enable to presence of the less abundant taxa to influence assemblage (dis)similarities (Clarke & Gorley, 2015). Hierarchical agglomerative clustering based on a Bray–Curtis similarity matrix was used to produce a dendrogram of station similarities. The SIMPROF routine was used as part of this procedure to delineate statistically different (at 10%) assemblage clusters. The fish taxa contributing the greatest amount to assemblage differences were identified using the SIMPER routine.

2.5.3 | Relationships with environment

A multivariate regression of environmental parameters on the fish MaxN data using redundancy analysis (RDA) was conducted. The RDA method is an extension of the multiple regression applied to multivariate response data. Being an asymmetric analysis, it allows a table of multiple explanatory variables (i.e. the environment) to be correlated with a table containing community data. The output, like that of any other ordination method, consists of principal axes in a reduced space, obtained by principal component analysis of a matrix of fitted response variables (MaxN) to explanatory parameters (environmental characteristics) by multivariate linear regression (Legendre & Legendre, 2012).

The environmental data were scaled for the RDA and fish community data were Hellinger-transformed following Legendre & Gallagher (2001). In a first model iteration, all environmental parameters were included. This model was appropriate as the variance inflation factor was <5 for all explanatory variables (except for distance to coast). Nevertheless, to simplify the model, a forward selection

method was performed which identified the explanatory variable with the highest R^2 for the first tested variable or the partial R^2 for the following tested variables. An explanatory variable was kept if the model was significantly different from the model version without the variable and if its inclusion improved the variance explained (higher R^2) by the model. The significance of each model was tested by permutation methods.

3 | RESULTS

3.1 | Habitats

The 87 successfully sampled stations ranged in depth from 3 to 49 m and encompassed three substrate types with eight different biogenic habitats including sponges, hard and soft corals, algal turf and seagrass (Table 1). However, stations were located predominantly on sea bed dominated by macroalgae, seagrass and sponges (15, 29 and 25 stations respectively). Fourteen stations were located across the five marine reserves: Rachette, Petit Piton and Gros Piton in the SMMA and Anse Cochon and Anse La Verdure in Soufrière to Marigot Bay region (Figure 1).

3.2 | Species distributions

Following truncation of the fish data, in the 87 stations a total of 5,921 fish were observed from 120 taxa across 22 families. Of these, six (Bothidae, Dasyatidae, Gobiidae, Kyphosidae, Labridae (juveniles) and Paralichthyidae) were identified to family in the final dataset, eight taxa were identified to genus while the remaining 106 taxa were described to species level. The most taxonomically diverse families were the carnivorous serranids (Serranidae; represented by seven genera), which includes sea basses and groupers; marine angelfish, or perciforms (Pomacanthidae), represented by six genera; and Labridae (wrasse), represented by five genera.

A large number of fish species were scarce and observed very sporadically. For example, 28 fish taxa were observed at only one station, while a further 13 were observed at two stations. Meanwhile, the most ubiquitous fish taxa observed were *Canthigaster rostrata*, present at 54 (or 62%) of the stations; juvenile Labridae (53% of the stations); *Stegastes partitus*, identified at 51% of the stations; *Acanthurus* spp., identified at 45% of the stations; and *Halichoeres gamoti*, observed at 41% of the 87 stations (Figure S1). *C. rostrata* showed greatest density in the Soufrière to Marigot Bay, a region where *S. partitus* and *Acanthurus* spp. were generally not observed.

While less ubiquitous, a small number of taxa were relative numerical dominants across the survey area. Notably, the two damselfish species, *Chromis multilineata* and *Chromis cyanea*, displayed a total MaxN across all stations of 1,443 and 558 respectively. The distributions of these two taxa (Figure S1) highlight that, although not widespread across the survey area (being

observed at 21% and 16% of stations respectively), they possess very high localized abundances.

3.3 | Fish assemblages

No fish were observed at one station near the entrance to Castries Harbour in the North of Marigot Bay region, while only two fish taxa were observed at a further four stations (Figure 2). Taxa number and total MaxN were generally highest in the south of the study area within the SMMA region (Figure S2), and four of the five most diverse stations (>32 taxa observed) and the five highest MaxN stations (MaxN >220) were located within this region. In contrast, the Soufrière to Marigot Bay and the North of Marigot Bay regions to the north contained more species-poor stations (lowest number of taxa) and lowest total fish abundances (Figure 2). However, it is apparent that the stations with the lowest number of taxa were generally those with high assemblage evenness (Pielou's J ; Figure 2). The number of stations located in each of the three regions (Table 1) was insufficient to sample all fish species present, although this bias was more or less equal across all three regions (Figure S3).

Clustering of the fish assemblage data resulted in a total of 12 significantly distinct fish assemblages, although five of these were represented by a single station, i.e. were outliers (Figure S4). The taxa defining each of these cluster groups (excluding outliers) are presented in Table 2. The main defining taxa of cluster I , the *C. multilineata*, was not a key taxon of any other cluster. Similarly, juvenile Labridae were influential in defining only cluster K (the most

commonly distributed cluster) during the clustering procedure. Clusters I and J were defined predominantly by a wider range of taxa (10 and eight taxa respectively contributed to the first 60% of cluster identity) relative to other clusters such as B and C where 60% of the cluster group was defined by two taxa. *Malacanthus plumieri* was a key defining taxa of cluster B only, a feature which undoubtedly contributed to this cluster group being the most distinct.

The geographical distributions of the various assemblage cluster groups (excluding outliers) show distinct spatial patterns (Figure 3). While stations whose assemblages reflected clusters B and C were largely found in the north of the survey region, most of the stations representing cluster I were located in the southern part of the study area. Meanwhile, clusters J , K , and L were generally observed to be more or less widespread across the region and all assemblages sampled within the various marine reserves (i.e. clusters I , J , K and L) were also found to be present outside of reserve boundaries.

3.4 | Relationships with environment

The model containing all environmental parameters was statistically significant ($p < 0.001$). Total variance in fish assemblage data was partitioned into constrained and unconstrained fractions; the constrained fraction, i.e. variation explained by the environmental parameters, was 37.5%. However, this value is artificially inflated by random correlation by the explanatory variables (Peres-Neto et al., 2006). Following an R^2 correction, the adjusted R^2 of the model was reduced to 17.0%. The model simplification undertaken with the forward

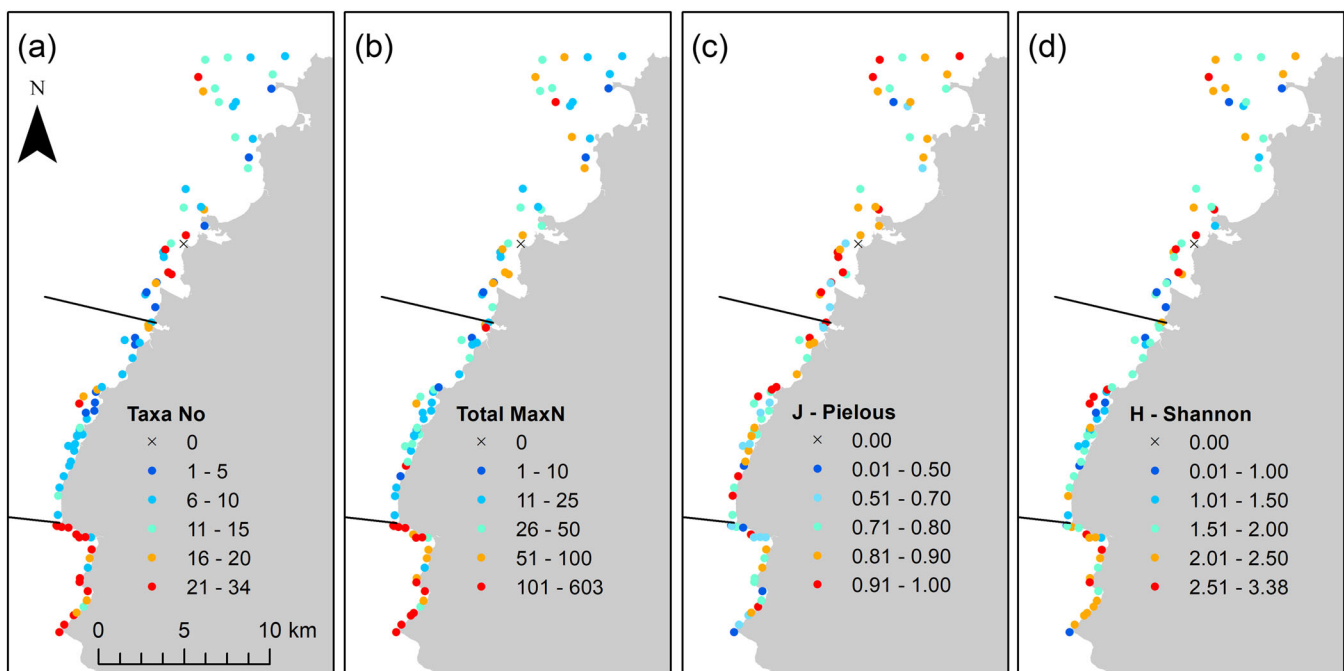


FIGURE 2 Univariate metrics of fish assemblage structure of the 87 stereo-BRUV stations. (a) Total taxa indicates total number of fish taxa observed; (b) total MaxN which reflects relative total abundance of each station; (c) Pielous (J) describes evenness; and (d) Shannon (H) represents a diversity measure

TABLE 2 Taxa contributing the most to characterizing the various fish assemblage cluster groups based on the data from the 87 BRUV stations. Outputs based on SIMPER routine (Figure S4). Taxa listed are those which cumulatively contribute to >60% of the total. Fish characteristic of clusters A, E, F, G and H are not presented as clusters only represented by a single station

Cluster	Main taxa	Trophic group	Mean MaxN	Percentage contribution	Cumulative percentage
Group B N = 4	<i>Halichoeres bivittatus</i>	Predator	2.8	47.6	47.6
	<i>Malacanthus plumieri</i>	Predator	1.0	32.2	79.9
Group C N = 6	<i>Pterois volitans</i>	Predator	1.2	52.7	52.7
	<i>Lutjanus buccanella</i>	Predator	5.2	20.2	72.9
Group D N = 2	<i>Acanthurus</i> spp.	Corallivore	20.0	32.9	32.9
	<i>Cephalopholis fulva</i>	Predator	4.0	20.5	53.4
	<i>Caranx ruber</i>	Predator	6.5	15.6	68.9
Group I N = 17	<i>Chromis multilineata</i>	Predator	80.0	8.7	8.7
	<i>Stegastes partitus</i>	Herbivore	14.5	8.4	17.1
	<i>Acanthurus</i> spp.	Corallivore	2.5	6.6	23.7
	<i>Halichoeres garnoti</i>	Predator	3.9	6.3	30.1
	<i>Scarus taeniopterus</i>	Herbivore	3.4	6.2	36.2
	<i>Thalassoma bifasciatum</i>	Predator	4.6	6.1	42.4
	<i>Sparisoma aurofrenatum</i>	Herbivore	4.1	4.8	47.2
	<i>Canthigaster rostrata</i>	Omnivore	1.4	4.8	51.9
	<i>Ocyurus chrysurus</i>	Predator	1.8	4.6	56.9
	<i>Chaetodon capistratus</i>	Predator	1.1	3.7	60.3
Group J N = 10	<i>Cephalopholis fulva</i>	Predator	2.9	11.7	11.7
	<i>Stegastes partitus</i>	Herbivore	5.5	10.5	22.2
	<i>Acanthurus</i> spp.	Corallivore	2.4	8.6	30.7
	<i>Sparisoma aurofrenatum</i>	Herbivore	1.4	8.2	38.9
	<i>Calamus pennatula</i>	Predator	0.8	6.7	45.6
	<i>Ocyurus chrysurus</i>	Predator	1.3	6.0	51.6
	<i>Chaetodon striatus</i>	Predator	1.3	4.8	56.4
	<i>Canthigaster rostrata</i>	Omnivore	1.2	4.7	61.1
Group K N = 32	Labridae (juveniles)	Predator	6.5	33.4	33.4
	<i>Canthigaster rostrata</i>	Omnivore	1.3	10.6	44.0
	<i>Halichoeres bivittatus</i>	Predator	1.6	6.5	50.4
	<i>Pterois volitans</i>	Predator	0.7	5.7	56.1
	<i>Xyrichtys splendens</i>	Predator	0.7	4.9	61.0
Group L N = 10	<i>Canthigaster rostrata</i>	Omnivore	2.3	41.5	41.5
	<i>Carangoides</i> spp.	Predator	2.3	29.2	70.7
	<i>Lutjanus buccanella</i>	Predator	5.2	20.2	72.9

selection method is shown in Table 3. The environmental parameters 'biogenic habitat', 'region' and 'depth' form the basis of the most parsimonious model explaining the main trends in fish distribution. This 'reduced' model (adjusted R^2) explains 15.0% of the total variation in fish distribution. Axes one and two respectively explain 41.7 and 17.6% (59.3% cumulatively) of the proportion of constrained eigenvalues (Figure 4), or 8.9% of the variance explained by the model. Table 3 indicates that the model captures at least one and potentially two of the most important environmental drivers of fish distribution, although it might not capture the major trend in the fish distribution. The first principal component (representing the model residuals)

represents only 7.0% (Figures S5 and S6), however, no major trends remain in the residual structure of the analysis. This implies that there is significant noise in the fish distribution data, and while the amount of variation explained by the model is small, the model performs well considering the amount of information contained in the data.

The 'distance' biplot (Figure 4), wherein the distance between stations and the centroids of the biogenic habitat variable (e.g. seagrass, soft coral, sponge) and region (e.g. North Marigot, Soufrière) parameters and the tip of the 'depth' arrow represents their similarity in Euclidean distance, shows four groups of stations along the x-axis. While stations within each group exhibit similar fish

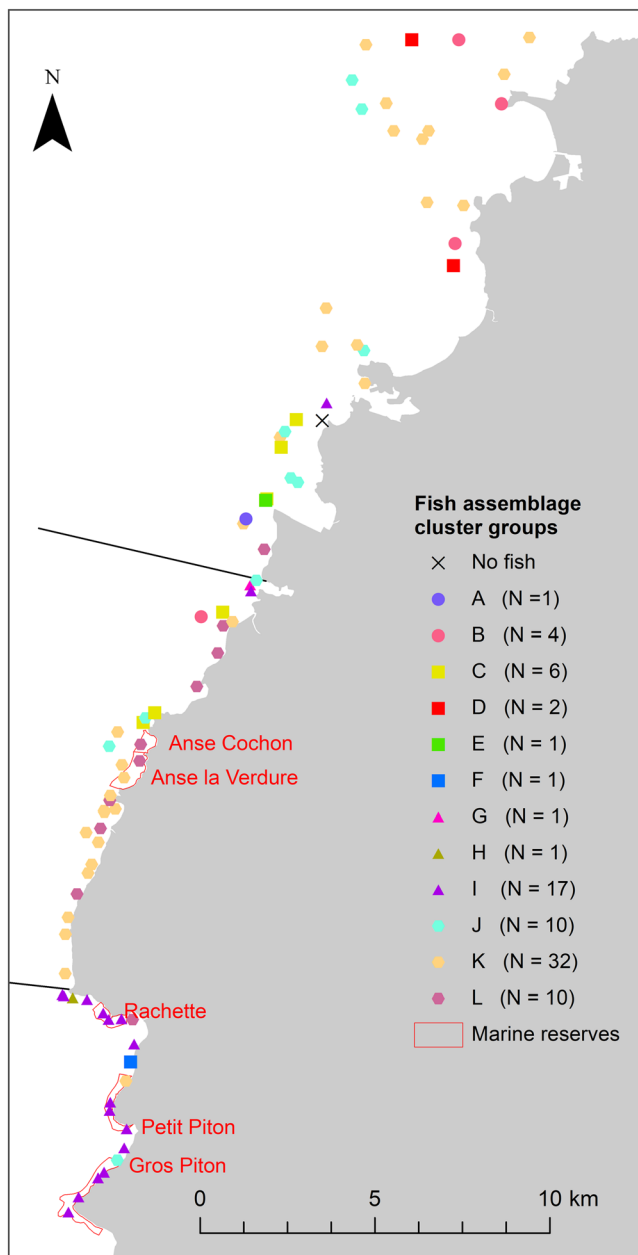


FIGURE 3 Distribution of the 12 significantly different (10%) fish assemblage cluster groups based on the data from 87 BRUV stations. The five marine reserves sampled are named in red text and the black lines indicate the boundaries between the three geographical regions

assemblages and are located in comparable habitats, fish assemblages and habitats vary between groups (Figure 4). Group 1 stations possess fish associated with hard coral in shallow regions and soft corals and gorgonians in slightly deeper waters. These stations are located within the Soufrière region and all the stations located within the Petit Piton, Gros Piton and Rachette Marine Reserves are in Group 1. Stations possessing the most contrasting fish assemblages to those of Group 1, located along the right-hand side with positive eigenvalues along the x-axis, are stations of Group 4 (Figure 4). These stations are located within seagrass beds and capture the assemblage observed at Anse La Verduce in shallow seagrass areas and that within the Anse Cochon Marine Reserve in deeper seagrass beds. Between the most divergent fish assemblage and habitats of Groups 1 and 4 are stations located in algal-dominated seabeds. The macroalgal stations within the North of Marigot Bay region are located within this group, and it is evident that the fish associated with macroalgal habitats in shallow areas slightly differ from those of algal turf and bacterial mat habitats in deeper waters. Finally, a number of stations which occur along a wide depth range have fish assemblages associated with sponges (Figure 4). This RDA distance plot, therefore, shows there is a relationship between observed fish assemblage structure and benthic habitat and depth. One station, located in very shallow water (bottom of the plot), possesses a fish assemblage that is not in accordance with its underlying environmental variables.

The correlation biplot (Figure 5) portrays the correlation between the explanatory (environment) and the response (fish assemblage structure) variables. The angles between the centroids (biogenic habitat and region) or arrows (depth) and the species arrows approximate the strength of the correlations. The plot indicates that a relatively small subset of fish taxa displayed a strong spatial distributional pattern that could be attributed to environmental differences. This is partly due to the fact that there was a very limited amount of spatial distribution in fish abundance even when not constrained by environmental factors (Figure S6). This further supports the notion of the presence of a significant amount of noise in the fish data, i.e. many fish show a more or less random distribution across the survey area. Very few species are strongly correlated with a benthic description or any other environmental driver. Nevertheless, *C. multilineata* and, to a lesser extent, *C. cyanea* and *S. partitus*, are strongly correlated with the hard coral. That is, their presence is generally limited to the stations located within the Soufrière region, and the Gros Piton, Petit Piton and Rachette protected areas. Some fish taxa including

TABLE 3 Results of the forward selection method using Akaike's Information Criterion (AIC), the starting point is an 'empty' model to which each variable is added in order of the highest adjusted R^2 improvement. Relevant variables are added until the model is not significantly (*) improved

Variable	R^2	d.f.	AIC	F	p-value
+ Biogenic habitat	10.77%	7	-23.4	2.4652	0.001*
+ Region	13.52%	2	-24.324	2.2392	0.001*
+ Depth	14.96%	1	-24.907	2.2872	0.001*
+ Distance to shore	15.88%	5	-21.785	1.1655	0.098

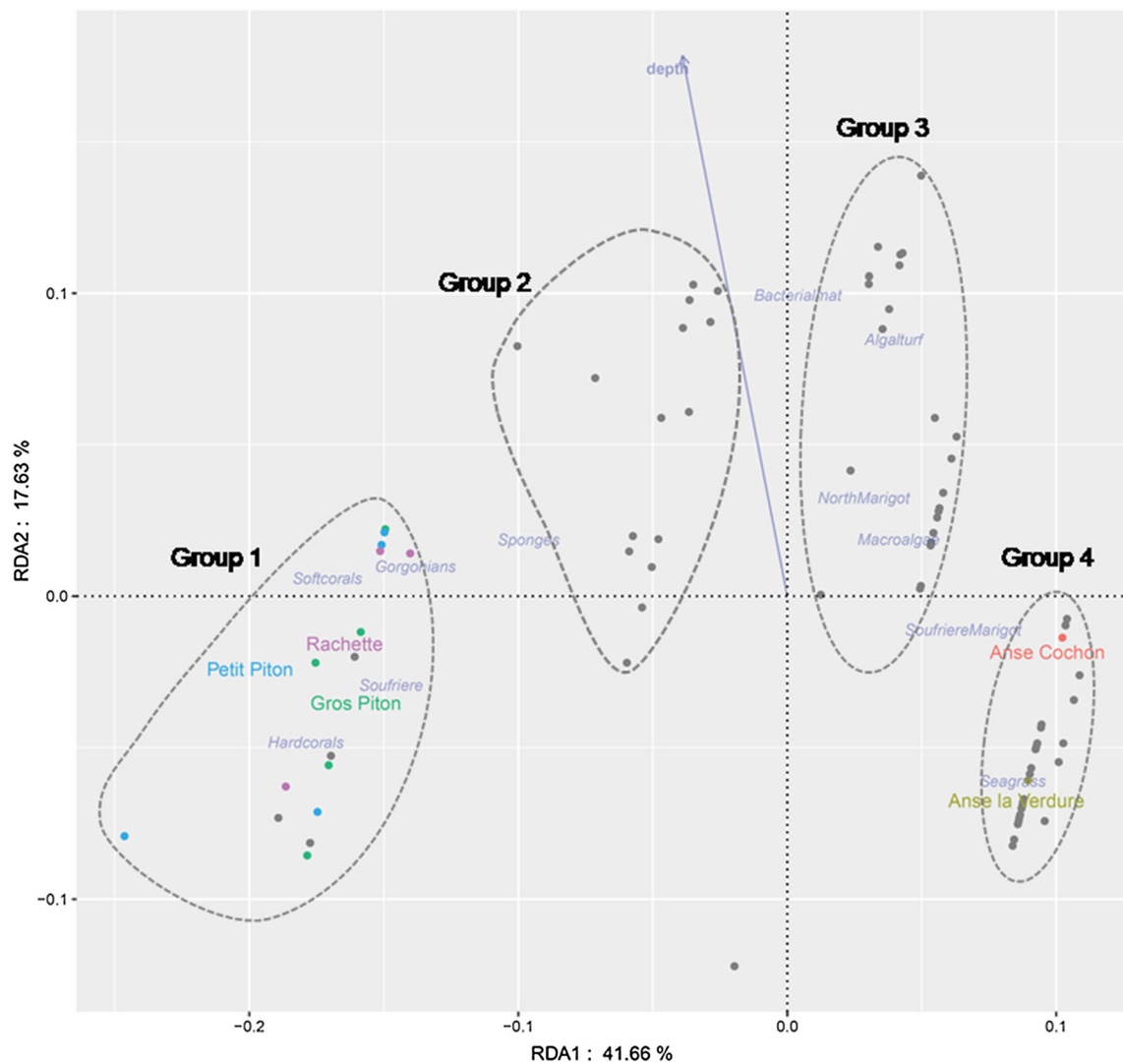


FIGURE 4 Results of the RDA with the most parsimonious model showing the stations similarity with the environmental parameters and biogenic habitat. The stations within the five marine reserves have been labelled and individually coloured to show their respective positions within the plot. The boundaries defining Groups 1–4 have been retrospectively superimposed to aid interpretation of the plot

H. gamoti, *S. taeniopterus* and *C. parrae* are associated with gorgonian habitats, soft corals and sponges, although their relationships do not appear as strong as those associated with hard coral. On the right-hand side of the plot depicting the soft-substrata areas, *P. volitans*, *M. plumieri* and *O. aurifrons* represent the few species correlated with algal turf and macroalgal habitats around North Marigot, while juvenile Labridae and *C. rostrata* show increased abundances within the shallow seagrass habitats of the SMMA region. The species contribution histogram insert plot in Figure 5 (for actual fish names see Figure S7) reveals that the majority of fish species display distribution patterns unrelated to environmental differences.

4 | DISCUSSION

There is a diversity of fish assemblages along the west coast of St Lucia which are spatially variable among regions and strongly

influenced by depth and biogenic seabed habitat. Demonstrating the nature of the relationships between fish assemblages and environmental drivers, as this study has achieved, is crucial if successful management and protection plans are to be implemented that protect the most diverse (Campos, Beldia II & Villarta, 2013) and representative communities (Stevens, 2002). The data revealed that fish assemblages are highly variable across the area with clear spatial patterns present, both in terms of the total abundances and diversity of fish, and in the distribution of particular fish species. The SMMA region in the south, which already has a number of designated conservation sites (Roberts, 2001; Hawkins et al., 2006), has a higher diversity and abundance of fish relative to the other areas surveyed (Figure 2 and Figure S2). In terms of univariate metrics, the other two regions, Soufrière to Marigot Bay and North of Marigot Bay, were more similar.

Most fishes were sporadically observed, with the most ubiquitous species (*Canthigaster rostrata*) observed at only 62% of the stations

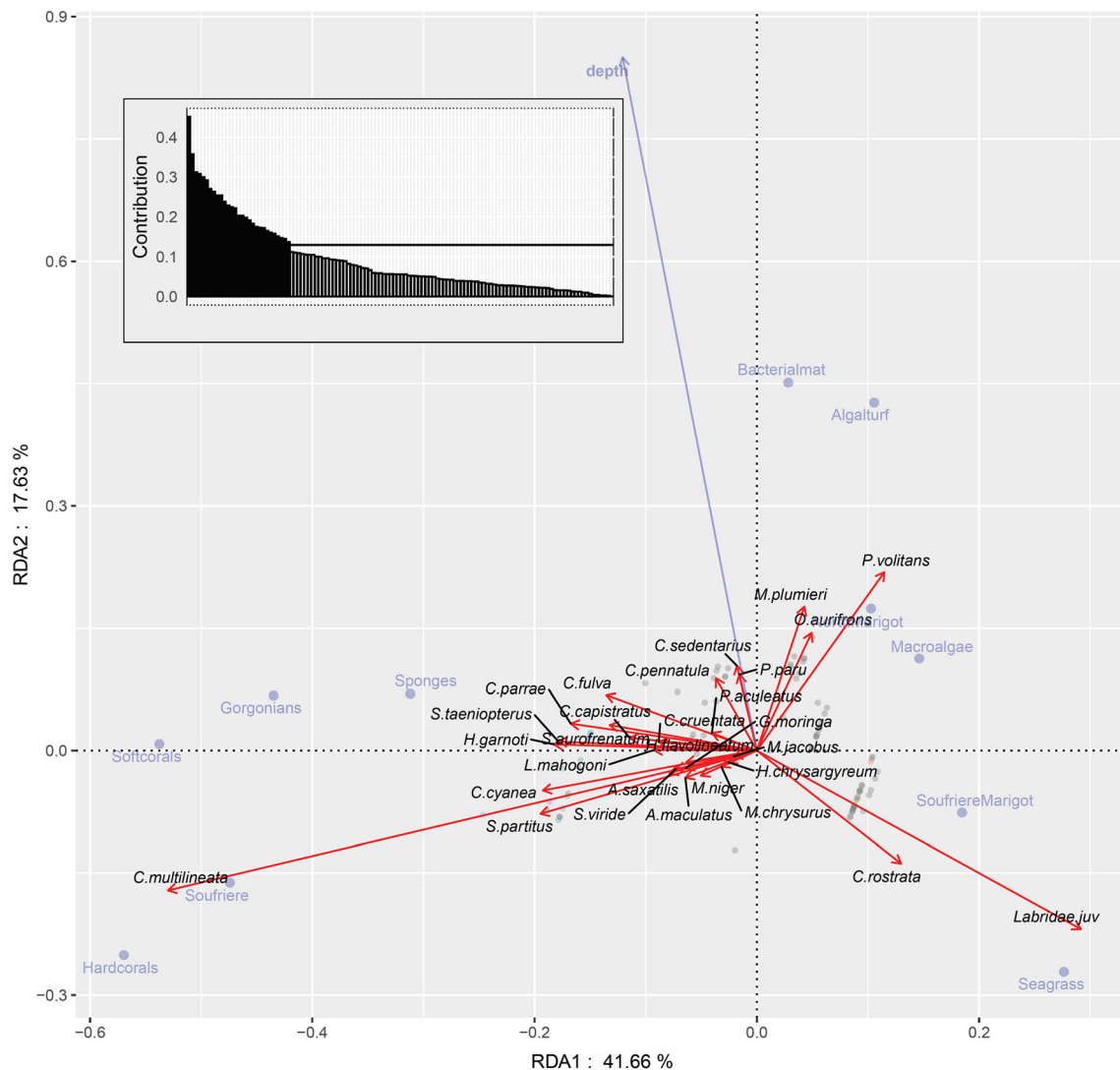


FIGURE 5 Results of the RDA with the most parsimonious model showing the correlation of the most contributory species of fish with the environmental parameters. The locations of habitat (as defined by phylogenetic dominance) and region within the RDA are also included. Insert shows the number of species included in the biplot (most contributory, in black) and those left out for clarity (less contributory, white). An enlarged figure of contribution values with species names is provided in Figure S7

while a third of taxa were observed at two or fewer stations. The general rarity of the fish species resulted in a diverse cluster of assemblages, some of which are driven by a few species at a limited number of stations (Table 2 and Figure 3). However, at least seven distinct fish assemblages occur along the west coast of St Lucia. The most species-rich of these assemblages was associated with complex reef habitats (dominated by corals or gorgonians) and restricted to the SMMA region in the south of the study area, which is well represented in current no-take reserves. Further north, two distinct assemblages were observed that are typical of seagrass habitats including most of the Soufrière to Marigot Bay region. As this region is currently under consideration for the establishment of additional marine reserves, it would be these habitats and fish communities that would be protected. Additional reserves implemented to represent those distinct seagrass assemblages may also benefit species targeted by

fisheries such as the snapper (*Lutjanus buccanella*) and jacks (*Carangoides* spp.).

Biogenic habitat, region and depth were important predictors of fish communities. The biogenic habitat on the seabed was the strongest predictor of fish assemblages, explaining ~11% of the variance (Table 3), with the stations separating into four general groups. These were: stations typical of complex reef-like habitats (those dominated by corals or gorgonians; Group 1), sponge dominated habitats (Group 2), habitats typical of flatter hard substrates (bacterial mats, algal turfs and macroalgae-dominated habitats; Group 3) and seagrass habitats (Group 4) (Figure 4). While the inclusion of region and depth described a further ~4% of variance in fish assemblages, the environmental data only explained 17% of the total variance. It is well established that seabed habitat is an important predictor of fish assemblages (Chabanet et al., 1997; Arias-González et al., 2006;

Komyakova, Munday & Jones, 2013), although the nature of such relationships is highly scale dependent (Yeager et al., 2017). Owing to limited data availability, the description of seabed habitat was derived from the BRUV field of view (i.e. dominant taxa, basic habitat classes and relief). With field of view limited to 8 m in one direction, it is likely that some stations were misclassified if the field of view was not representative of the wider area that may be within the foraging range for many species. Although habitat-fish assemblage relationships were observed within our data, these were primarily driven by a limited number of species (Figure 5 and Figure S7) and the majority of fish displayed a more or less random distribution based on the environmental variables included in our study. Improved habitat classification and mapping, through remote techniques such as multibeam echosounder swath mapping, may improve future marine spatial planning. Given our improved understanding of biodiversity-habitat associations in St Lucia, knowledge of the distribution of habitats could inform the optimal placement of further marine reserves.

This study did not set out to test the effectiveness of the current marine reserves. Rather, the aim was to characterize fish assemblages around the north west of St Lucia to assess whether the current marine reserves are representative of this region. The results confirm that a degree of relationship exists between fish distributions and seabed habitat types. However, across the five no-take marine reserves sampled in this study we observed that only a limited number of habitats were afforded protection. The SMMA region, a stretch of coastline that has been a priority for marine protection in St Lucia, was observed to be the most diverse of the three regions sampled, and the majority of diverse reef assemblages were located in this region (15 of the 17 stations clustered into group 'I'; Figure 3). RDA further supports that the SMMA region is primarily protecting only one type of fish community (Group 1 in Figure 4). This group was correlated with habitats dominated by hard or soft corals, or gorgonians. Further north, in the Soufrière to Marigot Bay region, different fish communities were observed within the sampled marine reserves compared with those of the protected areas of the SMMA. These stations were dominated by seagrass habitats and were generally similar in fish communities to one another (Group 4 in Figure 4). Seagrass is commonly described as a nursery habitat (Nagelkerken et al., 2002), and this was supported by the strong correlation observed in the data with juvenile Labridae.

Our data revealed that several unique fish assemblages are not currently afforded protection under St Lucia's marine reserve framework (Saint Lucia Fisheries Act 2001). The marine reserves have all been designated to protect either mangrove or reef features, yet our data show that unique assemblages are also associated with seabed habitats dominated by bacterial mats and algal turfs in the deeper stations and sponges and macroalgae in shallower stations (Groups 2 and 3 in Figure 4). In particular, the stations to the north of Marigot Bay that are currently open to various pressures, and in some of the deeper stations, these fish assemblages are different. While there are other marine reserves around St Lucia that were not sampled, it is unlikely these fish assemblages are present as the unsampled reserves are all inshore (Figure 1) and shallow relative to the samples classified

as Groups 2 and 3. Therefore, failure to protect these habitats may fail to cover all representative fish communities around St Lucia. Representativeness, and the concept that there is intrinsic value in conserving each type of habitat, not just the 'biggest, richest or rarest' (Stevens, 2002), is a decision support tool underpinning many MPA designs. Our data suggest that this is particularly the case as the often overlooked and less aesthetically attractive habitats are associated with distinct assemblages of fish.

While fish census data have previously been acquired within the SMMA, these data are of limited utility in aiding decisions regarding where to best locate future marine reserves to protect the most biodiverse assemblages. The stereo-BRUV data have extended our understanding of the nature and distribution of fish communities across the majority of the west coast of St Lucia and how they relate to seabed habitats. In doing so, the outcomes of this study will assist authorities to manage the marine environment of St Lucia by supporting the expansion of marine reserves to a greater range of depths and habitat types as this would result in the protection of a greater number of fish assemblages. In particular, our analysis has indicated that the north of the island, where no management measures are under consideration, possesses unique assemblages of fish and, therefore, further protection measures to protect specific assemblages associated with bacterial mat, algal turf, sponge and macroalgae habitats in this area should be considered.

This study has only used the biodiversity and abundance data derived from stereo-BRUVs, and not explored the fish length measurements. As habitat use and fishing pressure vary during different life stages of certain fish species, it is possible that the fish length and biomass data may provide further insights that support spatial planning, for example by identifying nursery habitats. Exploring the fish length data around St Lucia, based on this stereo-BRUV study, will be a focus of future work. In addition, further research to extend our understanding of fish distributions around the entire island of St Lucia may identify additional assemblages that have not been considered, particularly to the east on the more exposed windward side of the island. Nevertheless, the observed importance of habitat type and depth in explaining patterns of fish biodiversity is useful for marine spatial planning not only across St Lucia but also elsewhere. This study suggests that in the absence of direct fish observations, planning marine reserves which cover a broad spectrum of habitats and depths would ultimately benefit biodiversity representation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The author link is provided below:

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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